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Effects of simulated rat damage on yields of macadamia trees

M.E. Tobin*, A.E. Koehler and R.T. Sugihara
US Department of Agriculture, Denver National Research Center, P.O. Box 10880, Hilo, HI 96721, USA

Rattus rattus damages 5–10% of the developing macadamia (*Macadamia integrifolia*) nut crop each year, but the impact on yields of mature nuts has not been well documented. We evaluated the effects of simulated damage on yields of mature nuts at two locations on the island of Hawaii during the 1995 crop season. We removed 10 or 30% of the developing nut clusters from 5-year-old trees at 90, 120, or 150 days post-anthesis (dpa) and evaluated yields of mature nuts at 210–215 dpa. Removal of 10% of the crop load had no measurable effect on yields of mature nuts regardless of when damage was inflicted. Yields of trees with 30% of nut clusters removed differed from the control (no nut clusters removed) only when damage was inflicted at 150 dpa. These results raise questions about the cost-effectiveness of current rodent control programs, especially during early nut development. Growers may be able to tolerate damage to 10% of their developing nuts without suffering economic losses, and may be able to sustain losses as high as 30% provided that damage is incurred before 120 dpa. Damage control efforts should focus on reducing damage after 150 dpa. However, high rat populations and damage prior to 150 dpa might indicate the need to apply measures to reduce damage later in the crop cycle. Published by Elsevier Science Ltd

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Hawaii is the world's second leading producer of macadamia nuts. During the 1995 crop year, Hawaiian growers produced 52.5 million pounds net wet-in-shell macadamia nuts valued at $36 million (Hawaii Agricultural Statistics Service, 1996). A year-round mild climate and favorable growing conditions in Hawaii allow for prolonged flowering and harvesting seasons. Individual varieties of trees may produce flowers over a period of several months or more (Hamilton and Ito, 1984), and different varieties in an orchard flower at different times. Individual nuts take 210–215 days to develop from flowers to mature nuts, at which time they drop to the ground and are harvested either mechanically or by hand. As a result, many orchards have an almost continuous supply of nuts throughout the year.

Black rats (*Rattus rattus*) subsist and breed in Hawaiian macadamia (*Macadamia integrifolia*) orchards throughout the year on a diet composed largely of macadamia nuts (Tobin, Koehler and Sugihara, 1994). These rodents climb trees and feed on developing nuts from the time follicles are small, fleshy, unprotected fruits until kernels are fully developed and surrounded by hard shells. Most macadamia growers and industry specialists believe that this damage results in substantial economic losses to the Hawaiian macadamia industry (Fellows, 1982; Ooka, 1968; Tobin, 1992).

Many macadamia growers use rodenticide baits to control rat depredations in their orchards on the assumption that fewer rats result in less damage and, thus, higher yields. However, low levels of nut damage may have little or no impact on yield of mature nuts at harvest. In a study by Tobin *et al.* (1993), extensive and persistent snap trapping reduced rat populations and depredations on developing macadamia nuts but had little effect on subsequent yields of mature nuts.

During the 1994 crop season, we attempted to clarify the effects of rat feeding on developing macadamia nuts by simulating two levels of damage at two times during nut development and evaluating yields of mature nuts on individual clusters (Tobin *et al.*, 1996a). Both number of mature nuts per cluster and weight of mature nuts per cluster declined with increasing damage, indicating that individual clusters did not compensate for damage by retaining other nuts that might otherwise have dropped prematurely. However, macadamia trees translocate assimilates and other growth factors not only among nuts on the same cluster, but also among clusters on a branch and branches on a tree. Focusing on entire trees as experimental units might have provided a more realistic model for investigating compensatory mechanisms. Thus, during the 1995 crop season, we simulated damage and evaluated yields on entire trees.

*To whom all correspondence should be addressed, at: US Department of Agriculture, Denver National Research Center, P.O. Drawer 6099, Mississippi State, MS 39762, USA

Materials and methods

We conducted the study during the 1995 crop season at two locations on the island of Hawaii: MacFarms of Hawaii in South Kona District, on the drier south-western (leeward) side of the island, and Mauna Kea Macadamia Orchards in North Hilo District, on the windward side of the island. The trees at MacFarms, but not Mauna Kea, were irrigated. Both study sites had 5-year-old macadamia trees of variety 'Kau' (HAES 344) in their first year of commercial production.

We selected 84 trees of similar dimension, condition, and crop load at each study site for application of seven treatments: two levels of damage inflicted at three different times during nut development, plus an experimental control (no damage). We divided the trees into 12 blocks of seven trees each and randomly applied the treatments to the trees in each block.

We simulated damage by removing 10 or 30% of the nut clusters (racemes) from trees at 90, 120, or 150 days after peak anthesis. We counted all the nut clusters in each tree, calculated the number of clusters to be removed, and removed the clusters from several branches on different sides of each tree.

At harvest we collected all the nuts from the ground under each tree and placed them in an individually labeled bag. Later we husked, weighed, and counted the nuts in each bag before drying them in a convection oven at 49°C for 5–7 days. For all subsequent analyses we continued to use the entire sample collected from each tree at Mauna Kea but used 2.27-kg subsamples for each tree at MacFarms. We cracked the shells, extracted the kernels, and separated and weighed immature, unsalable (e.g. germinated, moldy, or damaged), and saleable kernels.

We performed mixed model ANOVAs with orchard and treatment as fixed effects and block within orchard as a random effect to detect differences among treatments in the number of mature nuts and weight of mature nuts produced per tree (SAS Institute, Inc., 1988). We performed a priori linear contrasts to detect overall differences among damage levels and between each of the 90-, 120-, and 150-day groups and the control group. We used Duncan's multiple range tests ($p < 0.05$) (Saville, 1990) to compare specific time × damage level combinations.

Results

Overall, production averaged 371 mature nuts per tree at the two sites. Production was similar between sites ($p = 0.50$) but varied among treatments ($F = 5.15$; d.f. 6, 126; $p = 0.0001$). Trees with 30% of the nut clusters removed produced fewer mature nuts (mean = 322) than did trees with either 0% (mean = 413 nuts) ($F = 8.50$; d.f. 1, 126; $p = 0.004$) or 10% (mean = 407 nuts) ($F = 18.55$; d.f. 1, 126; $p = 0.0001$) of the clusters removed (*Figure 1*). Production was similar between the 0 and 10% groups ($p = 0.96$).

Trees that had nut clusters removed at 90 or 120 dpa

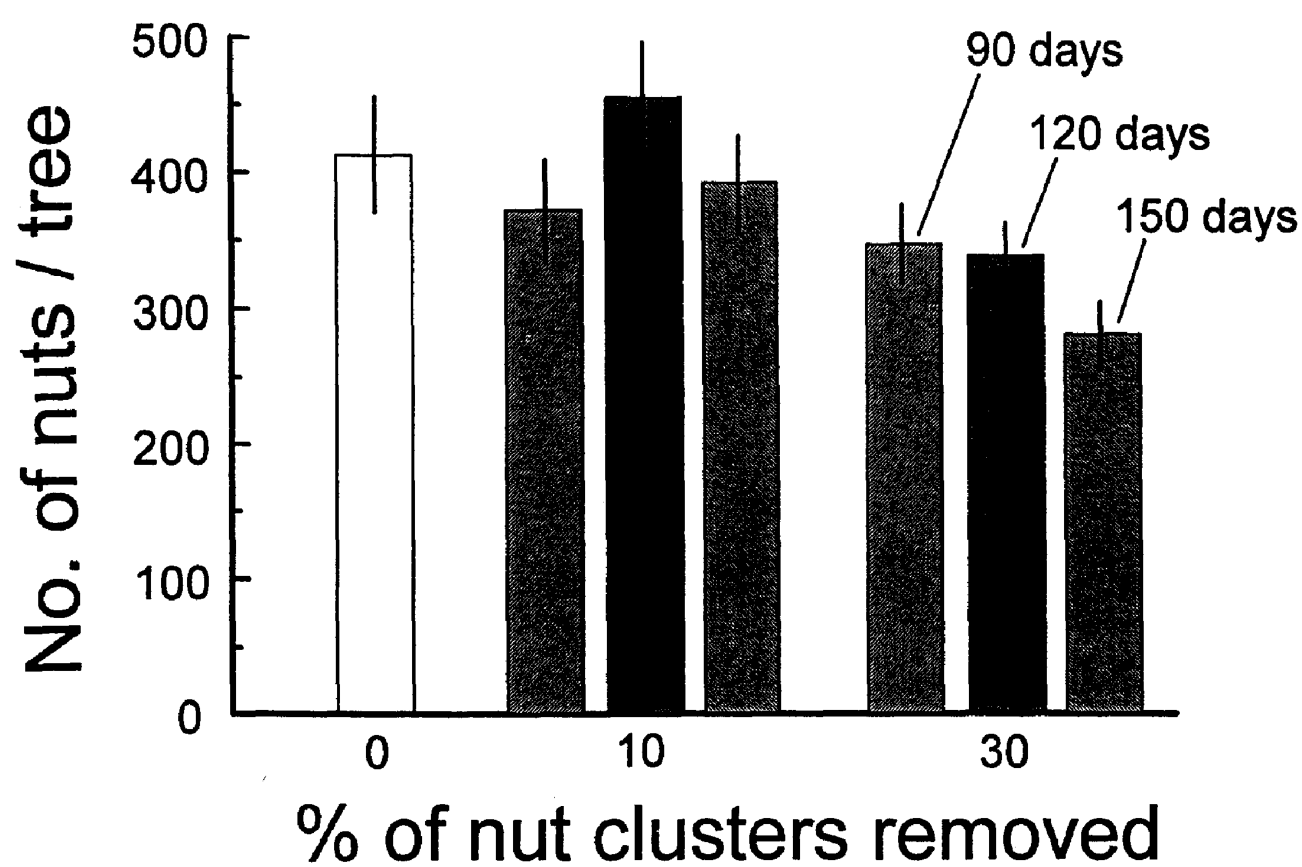

Figure 1. Mean number of mature nuts produced at two locations by 5-year-old macadamia trees of variety HAES 344. Rat damage was simulated by removing 10 or 30% of the nut clusters at 90, 120, or 150 days post-anthesis. The vertical line above each bar represents the standard error of the mean ($n = 24$)

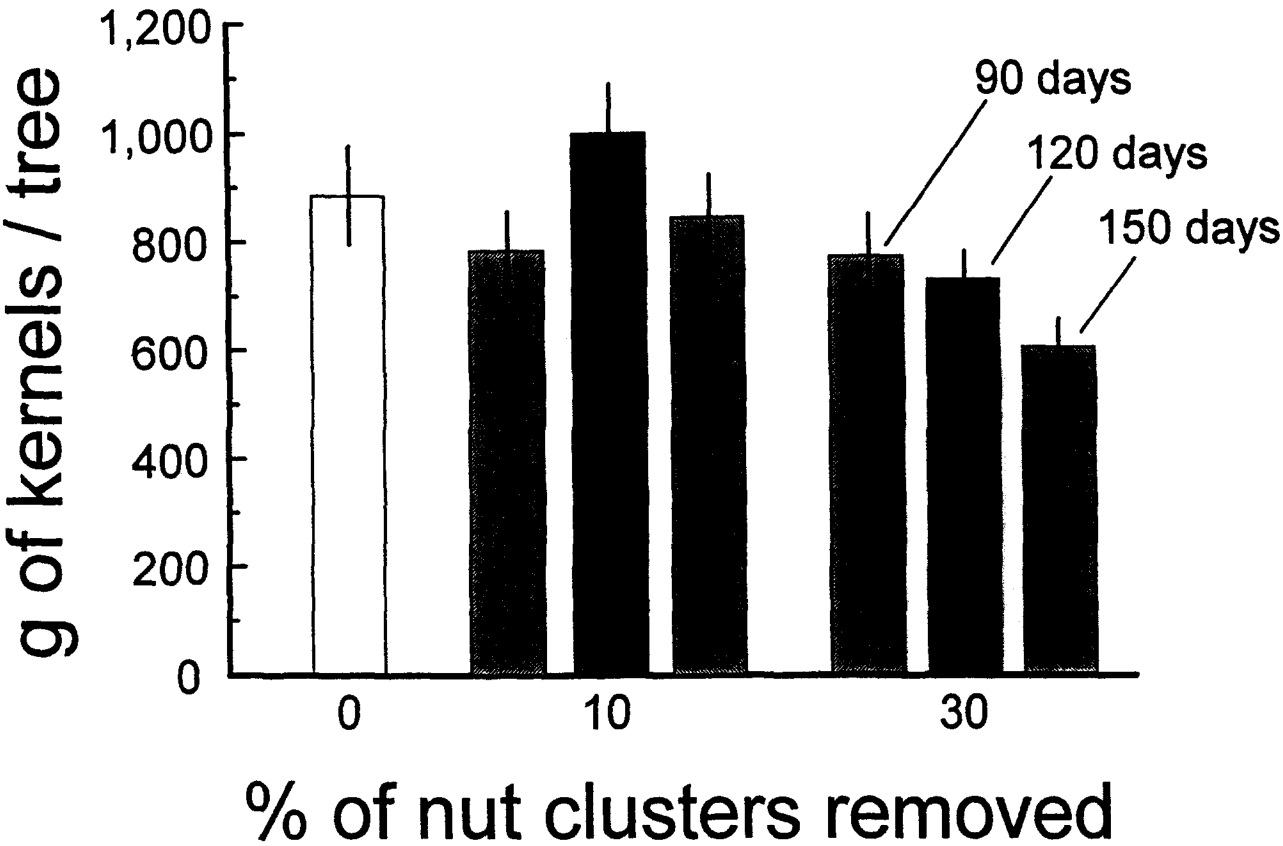

Figure 2. Mean weight of mature kernels produced per tree at two locations by 5-year-old macadamia trees of variety HAES 344. Rat damage was simulated by removing 10 or 30% of the nut clusters at 90, 120, or 150 days post-anthesis. The vertical line above each bar represents the standard error of the mean (n = 24)

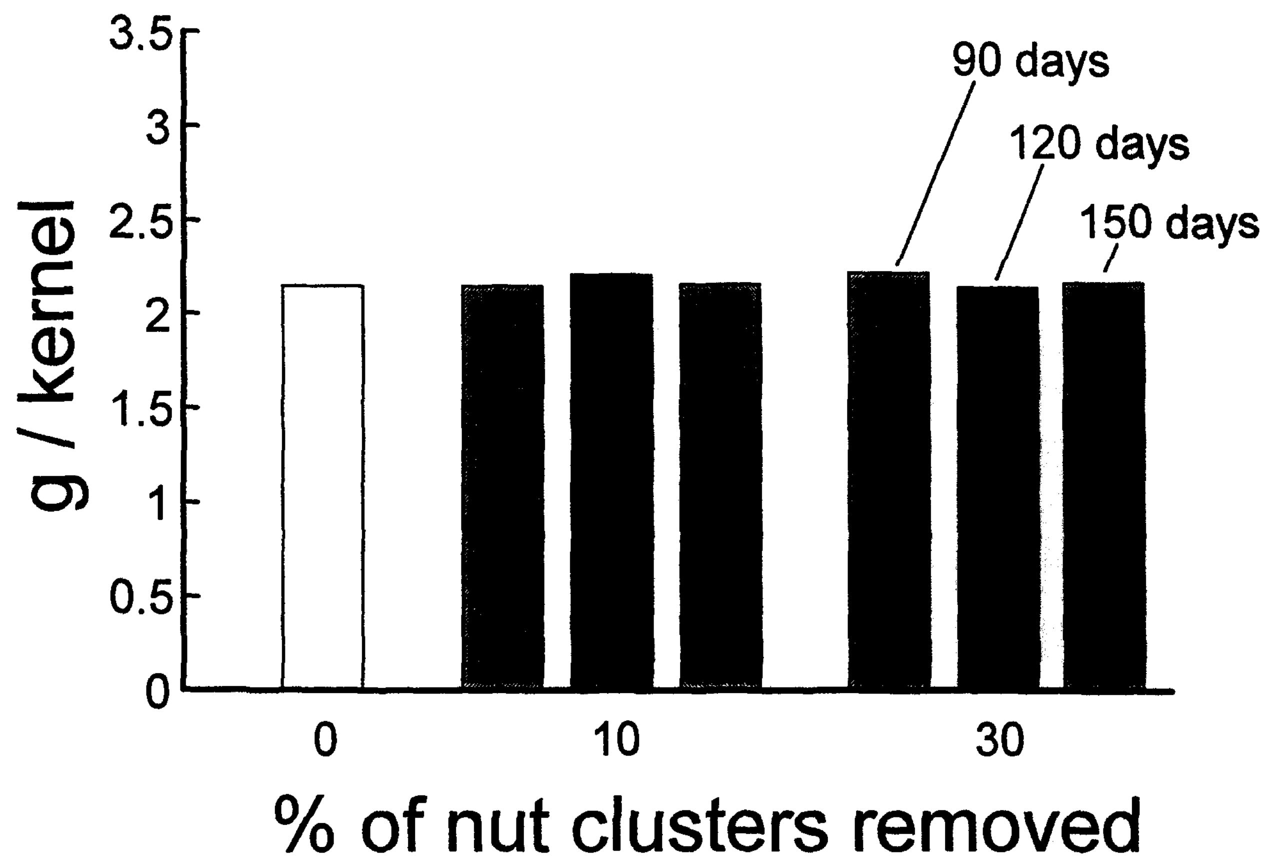

Figure 3. Mean weight of mature kernels produced at two locations by 5-year-old macadamia trees of variety HAES 344. Rat damage was simulated by removing 10 or 30% of the nut clusters at 90, 120, or 150 days post-anthesis. Standard errors of the means ranged from 0.03 to 0.07 (n = 24)

produced a similar number of nuts compared with the control group ($p = 0.12$ and $p = 0.71$, respectively) (*Figure 1*). Overall, trees damaged at 150 dpa produced fewer mature nuts than did trees in the control group ($F = 4.51$; d.f. 1, 126; $p = 0.036$). Only trees with 30% of their nut clusters removed at 150 dpa produced significantly fewer nuts than the control group.

The weight of mature nut kernels produced per tree averaged 801 g and was similar at the two sites ($p = 0.25$), but differed among treatments ($F = 5.16$; d.f. 6, 126; $p = 0.0001$) (*Figure 2*). Overall, trees that had 30% of their nut clusters removed produced a lower weight of mature kernels (mean = 700 g) than did trees in either the control (mean = 885 g) ($F = 7.33$; d.f. 1, 126; $p = 0.008$) or the 10% (mean = 876 g) ($F = 16.28$; d.f. 1, 126; $p = 0.001$) groups. The weight of mature kernels produced per tree did not differ between the control and 10% damage groups ($p = 0.94$).

The weight of mature kernels produced by trees with nut clusters removed at either 90 or 120 dpa was similar to that of trees in the control group ($p = 0.15$ and $p = 0.80$, respectively). Trees damaged at 150 dpa produced a lower weight of mature kernels than did trees in the control group ($F = 4.03$; d.f. 1, 126; $p = 0.047$). Only trees with 30% of their nut clusters at 150 dpa differed significantly ($p < 0.05$) from the control group.

We saw no treatment effect on average kernel weight or the percentage of harvested nuts that were immature. Mature kernels were significantly larger (mean = 2.44 g) at the MacFarm site than at the Mauna Kea site (mean = 1.92 g) ($F = 268.86$; d.f. 1, 126; $p = 0.0001$), but level and timing of damage had no affect on kernel weight ($p = 0.63$) (*Figure 3*). Likewise, there were proportionally fewer immature nuts at the MacFarms site (mean = 3.2%) than at the Mauna Kea site (mean = 5.2%) ($F = 10.73$; d.f. 1, 126; $p = 0.004$), but level and timing of damage had no effect on the percentage of harvested kernels that were immature ($p = 0.47$).

Discussion

Rats damage 5–10% of the developing macadamia nut crop in Hawaii (Fellows, 1982; Ooka, 1968; Pank *et al.*, 1978; Tobin *et al.*, 1993). Most researchers have assumed that such damage results in correspondingly proportional reductions in yields (Barnes, Loebel and Grange, 1989; Fellows, 1982; Pank *et al.*, 1978; Tobin, 1992; Turner, 1993). However, our results indicate that the impact of such levels of rat depredations on yields of mature nuts may be negligible, depending upon when the damage occurs. Removal of 10% of nut clusters, even as late as 150 dpa, had a negligible effect on yields of mature nuts. Removal of 30% of nut clusters significantly reduced yields of mature nuts when damage was inflicted at 150 dpa, but had only a marginal effect on yields when damage was inflicted at 90 or 120 dpa.

The similar weights of kernels in all treatment groups demonstrate that the trees did not compensate for damage by producing larger nuts. The larger size of kernels at MacFarms than at Mauna Kea most likely was due to the greater amount of sunlight at the former location (A. Yamaguchi, Kau Agribusiness, Inc. and H. Brown, MacFarms, Inc., pers. commun.).

The reason for the greater incidence of immature nuts at Mauna Kea is unclear but could also be due to the greater cloud cover, and thus less sunlight, at this site (A. Yamaguchi, pers. commun.). The percent of nuts that were immature did not appear to be affected by premature removal of nut clusters.

Macadamia trees exhibit apparent compensatory growth also in response to insect feeding on developing nuts. Jones and Tome (1993) reported that Koa seedworm and lychee fruit moth (*Cryptophlebia* spp.) damage to maturing macadamia nuts had little effect on yields unless > 25% of the nuts were damaged.

Coconut trees (*Cocos nucifera*) may also compensate for rat damage. Williams (1974) reported that production of harvestable nuts did not decline when coconut trees were artificially damaged, and he postulated that trees responded to damage by decreasing late immature nutfall. However, Reidinger and Libay (1980), in a different area with higher rat populations, reported a dramatic increase in coconut production when rat populations and damage were reduced, and they concluded that the effects of rat depredations on yields was far greater than could be predicted by measuring fallen, damaged nuts. Clearly the relationship between rat damage and coconut production is complicated and needs further study.

Sedgwick, Oldemeyer and Swenson (1986) reported that sunflowers (*Helianthus annuus*) may compensate for bird damage. Seedheads damaged by birds during early seed development had higher yields of undamaged sunflower seeds than heads damaged later in the season. They interpreted this as indicating that there was a period of maximal response to damage when plants are best able to redirect growth to seeds remaining in the head.

Beede *et al.* (1966) studied the ability of pistachios to compensate for nuts artificially removed at various times during nut development. They found that up to 40% of the nuts could be removed per cluster without significantly reducing the final number of filled nuts. They hypothesized that pistachio trees compensate for nut loss prior to shell hardening by setting and filling fruits that otherwise would fall off the tree.

Macadamia flowers and fruits abscise throughout the entire period of nut development, from anthesis through fruit maturity to 28–30 weeks later (Sakai and Nagao, 1984). A typical macadamia nut cluster produces 200–300 flowers, of which usually < 1% develop to full nut maturity (Sakai and Nagao, 1984). This high rate of premature nut abscission is a major constraint on nut production (Nagao and Hirae, 1992) and has been the focus of much research aimed at increasing fruit set and yields (Nagao *et al.*, 1982; Nagao and Sakai, 1990; Ueunten, 1989; Williams, 1980).

Most studies of premature macadamia nut drop have focused on the early stages of nut development, when the majority of premature nut drop occurs (e.g. Nagao *et al.*, 1982; Nagao and Sakai, 1990; Ueunten, 1989; Williams, 1980). Nuts do not begin accumulating significant amounts of high-energy fatty acids until after about 90 dpa (Cavaletto, 1980). It is at this time that nuts probably become most susceptible to damage by rats. We are not aware of any other studies that have evaluated the effects of nut loss after 90 dpa.

The growth and nut-bearing capacity of macadamia trees is limited by the availability of nutrients and stored carbohydrates (Cormack and Bate, 1976; Stephenson, Gallagher and Rasmussen, 1989). Nagao and Hirae (1992) reported that macadamia trees had similar yields over a 4-year period despite differing flowering intensities. Trees that initially had more flowers or immature nuts experienced higher premature abscission, leading the authors to conclude that the macadamia trees produced a surplus of flowers but were limited in the number of nuts they could bring to full maturity. Much of the damage caused by rats might be removal of 'excess' nuts.

Macadamia fruit growth and abscission are complex, dynamic processes that undoubtedly are influenced by the variety, age, and condition of the tree. We conducted the current study with young trees that were in their first year of commercial production and had a relatively synchronous flowering and nut maturity. As trees age, they usually flower over a longer period and produce a less synchronous nut crop. This asynchrony may provide older trees enhanced opportunities to reallocate nutrients from damaged nuts into later developing nuts. Repeating this experiment with 10–15-year-old trees would indicate whether the compensatory effect we observed with 5-year-old macadamia trees increases as the trees age.

Macadamia growers in Hawaii expend considerable effort to reduce rodent depredations in their orchards (Fellows, 1982; Ooka, 1976; Tobin, 1992;). Our results raise questions about the cost-effectiveness of control programs conducted during early nut development. Growers may be able to tolerate damage to 10% of their developing nuts without suffering economic losses, and they may be able to sustain losses as high as 30% provided that the damage is incurred before 120 dpa. More study is needed to evaluate the effects on yields of damage inflicted after 150 dpa. We predict that progressively less compensation occurs after 150 dpa, and that rat damage has a correspondingly greater economic impact.

We are not aware of any studies that have assessed rat damage inflicted to macadamia nuts during different times of the crop cycle but suspect that rat depredations usually increase during the later stages of nut development, after nuts have accumulated appreciable amounts of high energy oils. A recent radio-telemetry study confirmed that rats tended to forage in trees with relatively mature nuts (Tobin *et al.*, 1996b), and the present study indicates that damage control efforts should focus on reducing damage at this time because trees may be least able to compensate for damage to developing nuts. None the less, high rat populations and damage prior to 150 dpa, although having minimal impact on yields, might indicate the need to apply measures to reduce damage later in the crop cycle.

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